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## New Species and Combinations in *Heterotaxis* Lindley (Orchidaceae: Maxillariinae)

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**ABSTRACT.** Two undescribed species were detected while conducting a phylogenetic study of *Heterotaxis* (Orchidaceae: Maxillariinae): *H. fritzii* Ojeda & Carnevali from western Ecuador and *H. schultesii* Ojeda & G. A. Romero from the Amazon basin of Colombia and Brazil. These two species are described and illustrated, and their affinities are discussed. The first novelty is related to *Heterotaxis sessilis* (Swartz) F. Barros but the leaves are triquetrous, fleshier, and much narrower, while *H. schultesii* is similar to *H. villosa* (Barbosa Rodrigues) F. Barros, but with narrower, more coriaceous leaves and orange-red flowers. Six species are transferred to *Heterotaxis*: *H. discolor* (Loddiges ex Lindley) Ojeda & Carnevali, *H. equitans* (Schlechter) Ojeda & Carnevali, *H. maleolens* (Schlechter) Ojeda & Carnevali, *H. microiridifolia* (D. E. Bennett & E. A. Christenson) Ojeda & Carnevali, *H. santanae* (Carnevali & I. Ramírez) Ojeda & Carnevali, and *H. valenzuelana* (A. Richard) Ojeda & Carnevali. In addition, a lectotype and an epitype are designated for *Camaridium equitans* Schlechter, while lectotypes are chosen for *Camaridium vandiforme* Schlechter and *Dicrypta irisphyta* Barbosa Rodrigues. Lastly, *Maxillaria valenzuelana* subsp. *angustifolia* J. T. Atwood is treated for the first time as a synonym of *Heterotaxis valenzuelana*.

**RESUMEN.** Se detectaron dos especies nuevas en un estudio filogenético de *Heterotaxis*: *H. fritzii*, de Ecuador occidental y *Heterotaxis schultesii*, de la cuenca amazónica de Brasil y Colombia. Estas dos nuevas especies son descritas, ilustradas y sus afinidades discutidas. La primera novedad está relacionada con *Heterotaxis sessilis* (Swartz) F. Barros pero las hojas son tríquetras, mas carnosas y angostas, mientras que *H. schultesii* es similar a *H. villosa* (Barbosa Rodrigues) F. Barros, pero con ho-

jas más angostas y coriáceas y flores naranja rojizo. Otras seis especies son transferidas a *Heterotaxis*: *H. discolor* (Loddiges ex Lindley) Ojeda & Carnevali, *H. equitans* (Schlechter) Ojeda & Carnevali, *H. maleolens* (Schlechter) Ojeda & Carnevali, *H. micro-iridifolia* (D. E. Bennett & Christenson) Ojeda & Carnevali, *H. santanae* (Carnevali & I. Ramírez) Ojeda & Carnevali y *H. valenzuelana* (A. Richard) Ojeda & Carnevali. Adicionalmente, se selecciona un lectotipo y un epitipo para *Camaridium equitans* Schlechter y lectotipos para *Camaridium vandiforme* Schlechter y *Dicrypta irisphyta* Barbosa Rodrigues. Por último, *Maxillaria valenzuelana* subsp. *angustifolia* J. T. Atwood es tratada por primera vez como sinónimo de *Heterotaxis valenzuelana*.

**Key words:** *Heterotaxis*, Maxillariinae, Orchidaceae.

Maxillariinae is one of the most conspicuous and diverse subtribes of the Neotropical Orchidaceae. It is composed of 400 to 450 species (e.g., Atwood & Mora de Retana, 1999; Carnevali & Ramírez, 2003), approaching 650 species in other recent calculations (e.g., Dodson, 2002). They are common and widespread elements in humid Neotropical forests and range from southern Florida (U.S.A.) to northern Argentina, with centers of diversity in southern Central America, along the Andes, and in southeastern Brazil (Dressler, 1981, 1993; Carnevali, 1991; Senghas, 1993; Whitten et al., 2000).

Members of Maxillariinae are extremely variable in vegetative morphology and size, varying in height from 1 cm to 2 m. Plants bear heteroblastic pseudobulbs (i.e., of 1 internode) or lack pseudobulbs altogether and feature 1 to 2(to 4) leaves per stem or pseudobulb. Rhizomes are short, branching or

not, forming erect, ascendent, or pendulous plants. Plants are epiphytic or secondarily terrestrial in habit. Growth may be either monopodial or sympodial. Despite all this vegetative plasticity, the flowers are remarkably homogeneous in overall structure throughout the subtribe (Carnevali & Ramírez, 1989; Carnevali, 1991; Holtzmeier et al., 1998; Dodson, 2002). Thus, the phylogenetic relationships of the several morphologically recognizable groups within the subtribe and their circumscriptions have been difficult to ascertain, partially because the great vegetative plasticity of the group is not obviously associated with an equivalent, correlated floral variability.

Until recently, orchid systematists had recognized the following genera in the Maxillariinae: *Cryptocentrum* Benth., *Mormolyca* Fenzl, *Chrysocynis* Lindley & Reichenbach f., *Cyrtidiorchis* Rauschert, *Anthosiphon* Schlechter, *Pitiphyllum* Schlechter, *Trigonidium* Lindley, and *Maxillaria* Ruiz & Pavón (Dressler, 1993; Atwood & Mora de Retana, 1999; Dodson, 2002; Carnevali & Ramírez, 2003). However, recent phylogenetic analyses using DNA sequences (Whitten et al., 2000; Whitten, unpublished) have resulted in a broader understanding of the relationships within the subtribe and among some of the groups included within *Maxillaria*. The most striking result of these new analyses is, perhaps, evidence indicating that the large genus *Maxillaria*, as currently circumscribed, is grossly polyphyletic. Alternatively, the circumscription of the genus would have to be expanded in such a way as to be morphologically undiagnosable and ecologically and biogeographically meaningless, since it would include all members of subtribe Maxillariinae with conduplicate leaves. Furthermore, the circumscription of subtribe Maxillariinae has also recently been expanded to include subtribes Lycastinae and Bifrenariinae (Whitten et al., 2000), in disagreement with the currently accepted circumscription that in a narrow sense encompasses only species with conduplicate leaves, therefore excluding Lycastinae and Bifrenariinae (the plants of which bear plicate leaves).

Thus, relationships within subtribe Maxillariinae s. str. beg for a generic realignment to recognize generic aggregations that, besides being monophyletic, would be more manageable in size, morphologically diagnosable, and that would reflect ecological preferences and biogeographical patterns. The circumscriptions of some genera surely will require broadening, while other smaller monophyletic groups, most of them formerly included within *Maxillaria*, will deserve generic recognition (Ojeda,

2003; Whitten, unpublished; Ojeda & Carnevali, in prep.).

Among the several monophyletic groups recognized by the preliminary phylogenetic analyses there is a basal clade that can be identified by a combination of morphological features. One of the most conspicuous of them is the presence of fleshy flowers as opposed to the typically fibrous flowers of most members of the subtribe. Within this clade there are three monophyletic groups. One of them, *Heterotaxis* Lindley, has been recently reinstated (Barros, 2002), and this circumscription is strongly supported by our phylogenetic work that places *Heterotaxis* in a basal position in the phylogeny of *Maxillaria*, or of the conduplicate-leaved Maxillariinae, more closely related to other taxa (such as *Ornithidium* Salisbury, *Mormolyca*, and *Cryptocentrum*) than with the "core" *Maxillaria* (Ojeda et al., in prep.; Whitten et al., 2000; Whitten, unpublished) typified by *Maxillaria platypetala* Ruiz & Pavón (e.g., Dodson, 2002).

*Heterotaxis* comprises about eleven primarily epiphytic species ranging from the southeastern United States (Florida) and the Greater Antilles to Brazil, with most of the species occurring in Central and South America (Carnevali, 1991). As in *Maxillaria* s. str., the inflorescence in *Heterotaxis* is 1-flowered and emerges from the leaf axils. The flowers are yellow to orange or orange-red, with the labellum in some species being totally purple, or more rarely pinkish lips with calli varying in size and texture; in some other species the lamina of the labellum is basically yellow or orange with purple or reddish spots or blotches. The distinctly fleshy flowers are shared with the *Ornithidium* complex of *Maxillaria* (a related group of taxa that may also merit generic recognition). *Heterotaxis* is characterized by short rhizomes and laterally compressed, oblong pseudobulbs, which are unifoliate, and subtended by various leaf-bearing sheaths. Exceptions are *Maxillaria equitans* Schlechter, and *Maxillaria valenzuelana* (A. Richard) Nash, which exhibits a pseudomonopodial growth without pseudobulbs. Based on this growth habit difference, Hoehne (1947) proposed *Marsupiarina* based on *Maxillaria valenzuelana*, where he also included *Maxillaria equitans*.

It has been hypothesized (e.g., Carnevali, 1991) that *Maxillaria witsenioides* Schlechter (syn: *Marsupiarina witsenioides* (Schlechter) Pabst) also belongs in this group because of its monopodial growth habit with laterally compressed leaves. However, recent evidence from the internal transcribed spacers sequence (ITS) along with a detailed morphological re-evaluation of *M. witsenioides* (Ojeda & Carne-

vali, unpublished) clearly shows this taxon to be unrelated to the members of *Marsupiarina* and places the species as a member of a clade that includes *Maxillaria aciantha* Reichenbach f. and *Maxillaria notylioglossa* Reichenbach f. (N. H. Williams, unpublished).

*Heterotaxis* was based on a species described in 1826 by John Lindley as *Heterotaxis crassifolia*. This species was treated until recently as *Maxillaria crassifolia* (Lindley) Reichenbach f. (= *Heterotaxis sessilis* Lindley). The same concept was later redescribed by Lindley as *Dicrypta crassifolia* Lindley (Lindley, 1830). Although Lindley argued against his earlier generic concept, the *International Code of Botanical Nomenclature* (Greuter et al., 2000) should be followed in applying the Principle of Priority. Thus, the name to be used to refer to these taxa is the older *Heterotaxis* Lindley, sensu Lindley, 1826.

Most authors have treated members of this complex of taxa within a broadly circumscribed *Maxillaria* (e.g., Foldats, 1970; Carnevali, 1991; Senghas, 1993; McLeish et al., 1995; Christenson, 1999), although several had pointed out the possibility of generic recognition (e.g., Brieger & Illg, 1972; Illg, 1977; Carnevali, 1991; Carnevali & Ramírez, 2003) or had already segregated totally or partially the group into new genera or through the resurrection of older genera (e.g., Hoehne, 1947). The group had already been recognized as distinct in several features, including characteristics of pollinia and cytology (Carnevali, 1991) as well as by the fleshy flowers. Recently, Christenson (1999) based on morphological characters, recognized this aggregate of species as *Maxillaria* sect. *Iridifolia*. John T. Atwood (unpublished) recognized the *Heterotaxis* alliance that, together with sub-alliances *Crassifolia* and *Valenzuelana*, comprises the *Heterotaxis* complex. More recently, a paper published by Barros (2002) recognized *Heterotaxis* and transferred four Brazilian species of this complex. Finally, in the course of a systematic and phylogenetic study of the *Maxillariinae* in general and of the *Heterotaxis* complex in particular that was based on morphology, gross foliar anatomy, and DNA sequences (nuclear ITS1 and ITS2 regions), additional evidence was obtained that supports the idea that *Heterotaxis* deserves generic recognition (Ojeda, 2003).

The objective of this contribution is to describe two new species that were detected in the course of the systematic analysis of the genus *Heterotaxis*. We then proceed to formalize the nomenclatural novelties required to update the circumscription

and nomenclature of the genus, making six names available for general systematic and floristic usage.

***Heterotaxis fritzii* Ojeda & Carnevali, sp. nov.**

TYPE: Ecuador. Imbabura: Lita-Alto Tambo area, probably along the road from Lita to San Lorenzo, flowering in cultivation in Gainesville, Florida, U.S.A., 24 Feb. 2004, M. W. Whitten 2672 (holotype, FLAS). Figures 1, 2.

Species haec *H. sessili* (Swartz) F. Barros similis sed habito parviore, foliis triquetris proportione angustioribus brevioribus, callo parte anteriore farinoso differt; *H. santanae* (Carnevali & I. Ramírez) Ojeda & Carnevali in mentem revocans sed foliis triquetris proportione angustioribus, labello acuto recedit.

Plant caespitose, sub-terrestrial, presumably also epiphytic, erect, ca. 25 cm tall, rhizome unknown but presumably abbreviated; roots grayish, ca. 2 mm diam.; pseudobulbs small, 1–2 × 0.4–0.6 cm, narrowly ellipsoid, unifoliate, partially or totally hidden by sheaths of which the innermost 2 to 3 (to 4) on each side bear foliar blades. Leaves and the foliar blades of the sheaths distichous, 6–13 × 0.45–0.55 cm, thickly fleshy, linear-elliptic, subtriquetrous with the upper margins rounded (thus somewhat heart-shaped in cross section), unequally 2-lobed at apex, lobes obtuse, basally not constricted into a pseudopetiole; base and margins of leaves and sheaths dull green-yellow. Inflorescence one-flowered, ca. 4.5 cm long, borne on the leaf-sheath axils; floral bract 1.5 cm long, much shorter than ovary, the last bract of the peduncle surpassing the articulation of the pedicel to the ovary and pedicel; ovary and pedicel ca. 10 mm long, 3 mm thick. Flowers medium sized or small for the genus, ca. 17 mm long, fleshy, clear yellow-green; perianth segments subparallel to the column; sepals 16.5–17.5 × 4.5–5.5 mm, sub-similar with the laterals somewhat oblique, oblong-elliptic, acute; petals 14.5–15.5 × 2.4–2.6 mm, oblanceolate to spatulate, margin entire; labellum 14.5–15.5 × 4.5–5.5 mm, slightly 3-lobed, rhombic-ellipsoid in general outline, apex acute, basally cuneate, yellow with 2 series of large dark red or maroon spots or blotches that run parallel to the calli (4 to 7 on each side), articulated to the column foot; disc dull yellow, with two linear calli that are parallel to the main axis of the labellum, the basal callus is placed in the basal half of the disc, fleshy, the second callus is placed in the apical half of the disc and is farinose (mealy); column ca. 8 mm long, 2 mm thick, green-yellow, strongly arcuate, hemi-cylindrical, wider at base, with a poorly defined foot ca. 1 mm long; anther unilocular with papillose margin, ca. 3 mm long, dull yellow; pollinia 4, unequal. Fruits not seen.

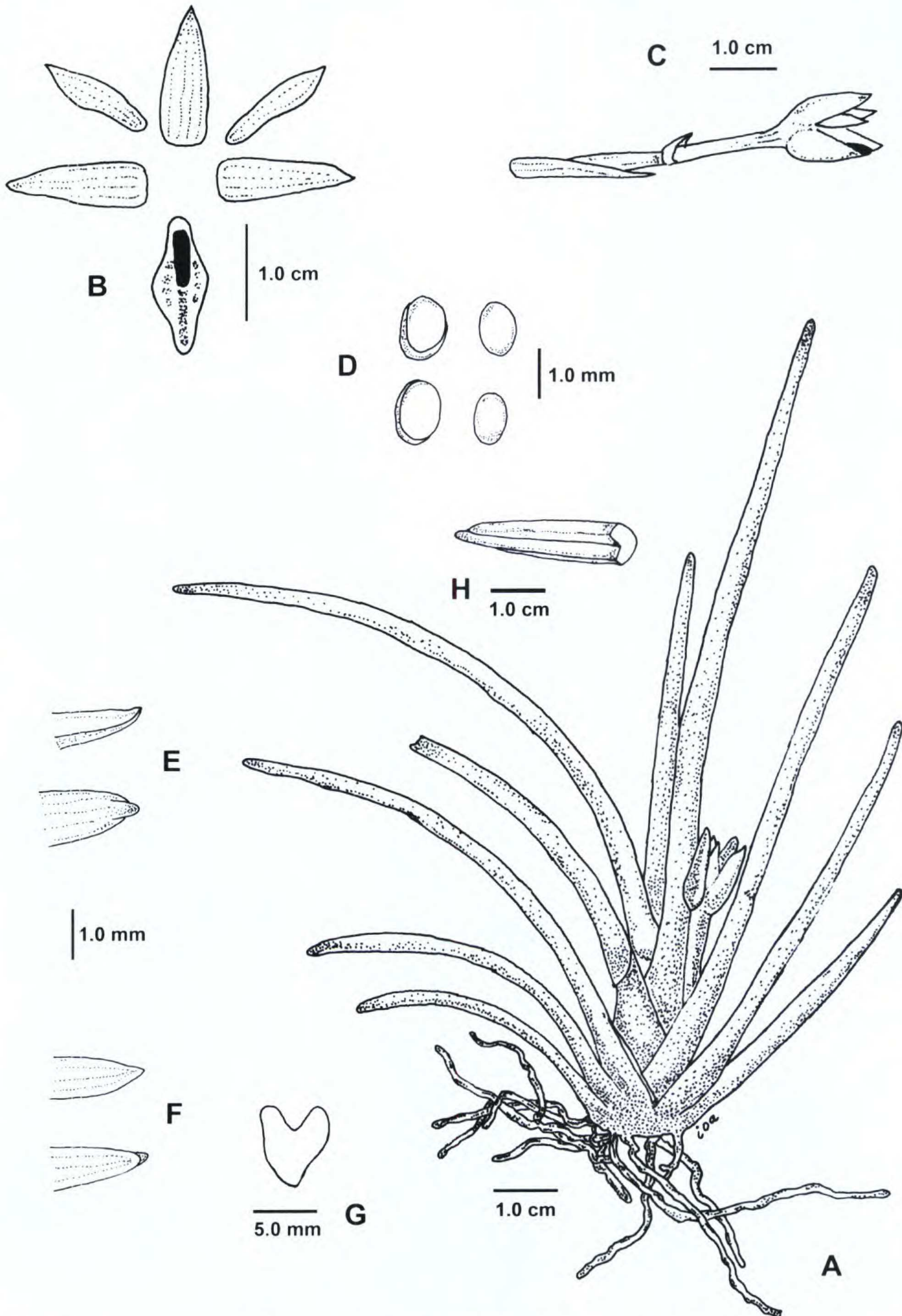


Figure 1. *Heterotaxis fritzii* Ojeda & Carnevali. —A. Plant habit. —B. Perianth. —C. Flower with peduncle and last two sheaths. —D. Pollinia. —E. Sepals from top: ventral and dorsal view. —F. Petals from top: ventral and dorsal view. —G. Leaf in cross section. —H. Apex of leaf. Drawn by Isidro Ojeda (based on paratype, Carnevali 3443, and supplemented with photographs).

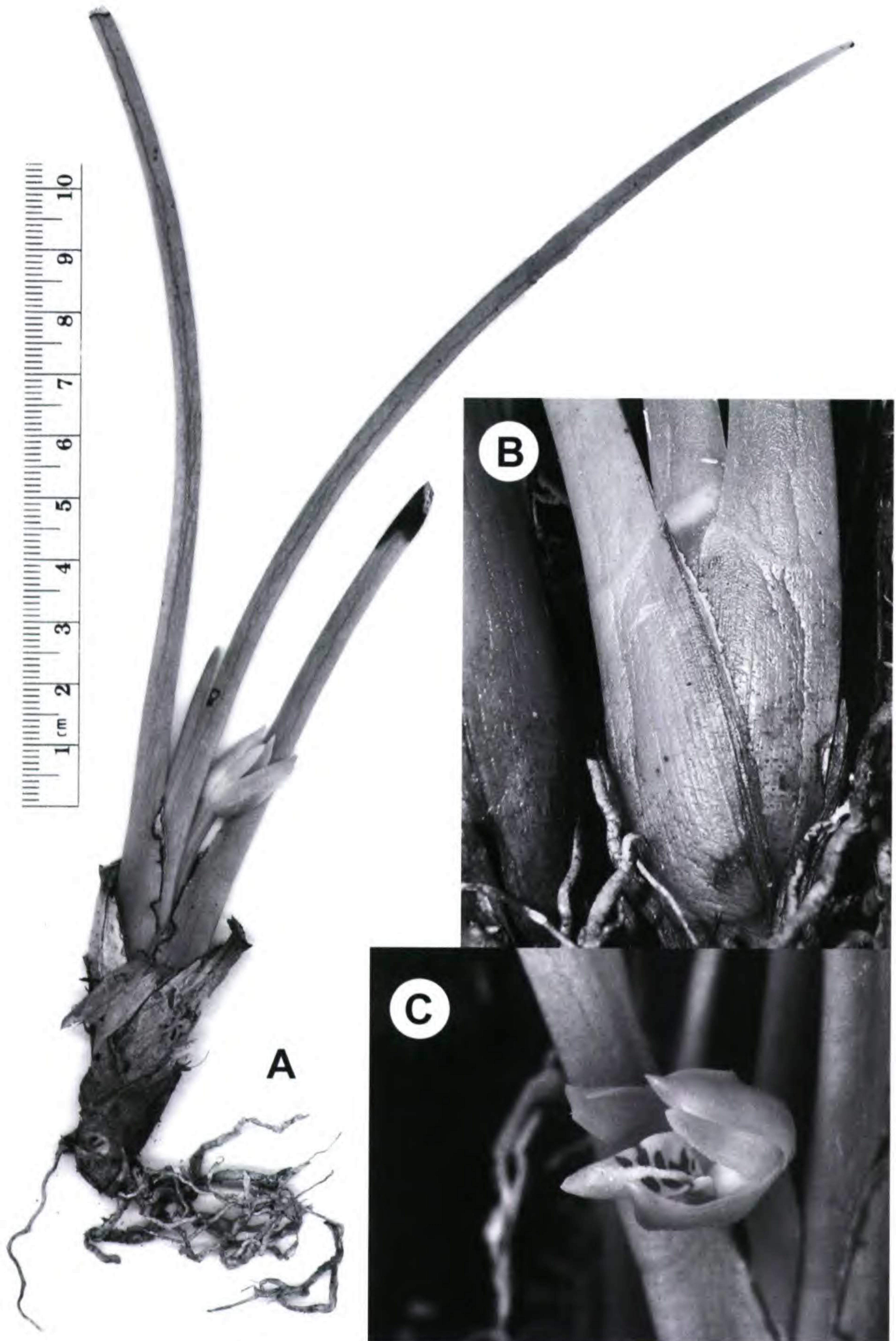


Figure 2. *Heterotaxis fritzii* Ojeda & Carnevali. —A. Plant habit. —B. Base of plant showing partially hidden pseudobulb. —C. Close-up of flower, showing the two calli of the labellum. Photographs by W. M. Whitten (based on living material later preserved as holotype).

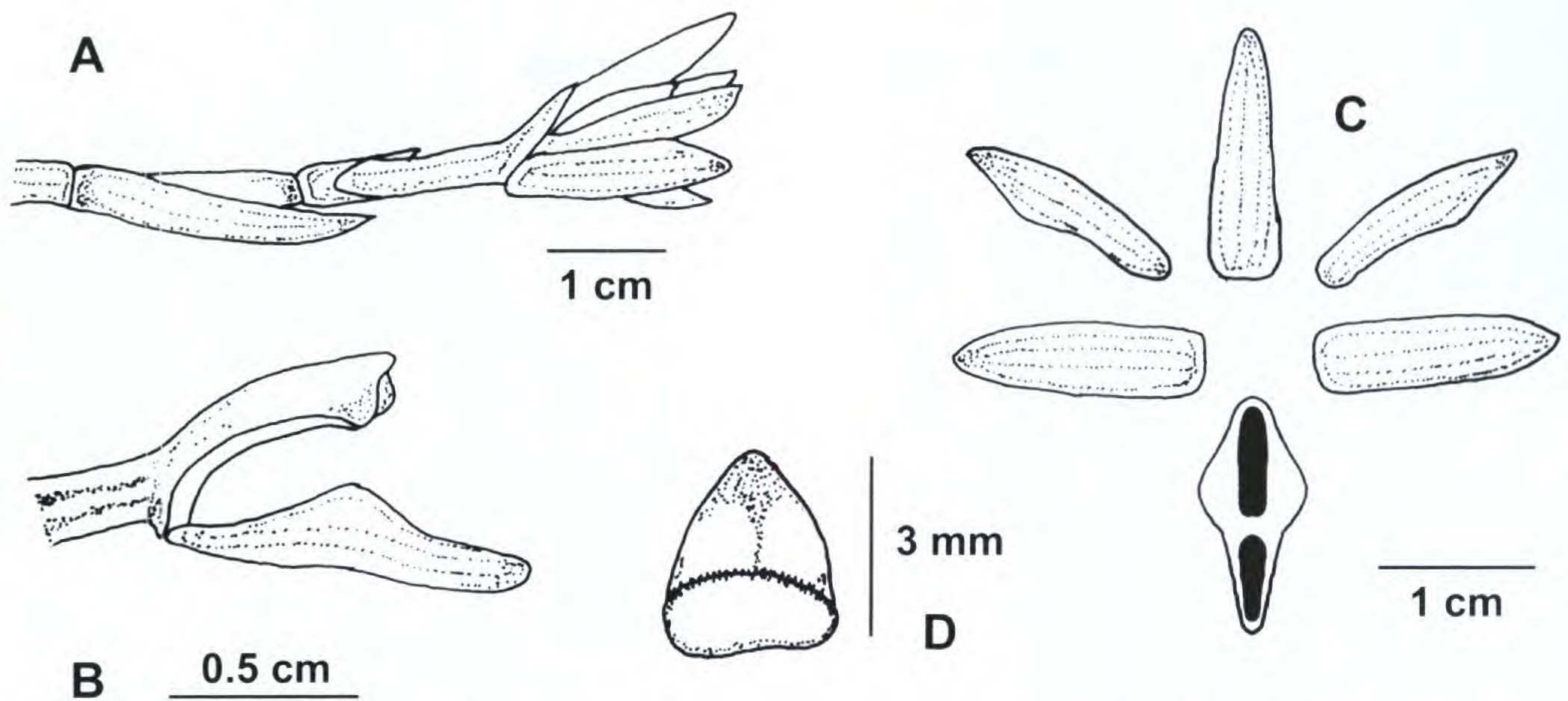


Figure 3. *Heterotaxis schultesii* Ojeda & G. A. Romero. —A. Flower with peduncle showing two last sheaths. —B. Column with labellum articulated. —C. Perianth. —D. Anther. Drawn by Isidro Ojeda (based on paratype *R. E. Schultes* & *I. Cabrera* 12788).

**Eponymy.** Named in honor of William Fritz of Union, Missouri, who cultivated a plant of this species for several years when he lived in St. Louis, Missouri.

Until recently, this species was only known from a 1994 collection made by one of us (Carnevali) and C. H. Dodson along the orchid-laden road from Lita to San Lorenzo, Imbabura, in western Ecuador. Subsequent trips to this locality by C. H. Dodson failed to reveal more plants. However, several plants of the species have recently been collected from the same general area and brought into cultivation. The holotype of the species was prepared from one of these plants. *Heterotaxis fritzii* at first looks morphologically intermediate between *H. valenzuelana* and *H. sessilis*, neither of which grows nearby. Both *H. valenzuelana* and *H. sessilis* have broader leaves than those of *H. fritzii*. *Heterotaxis sessilis* is only known in Ecuador from Los Rios and Guayas at lower elevations and drier areas (e.g., *Haught* 3128 (AMES, MO), but these Ecuadorian collections might be referable to the entity described as *Maxillaria gatunensis* Schlechter, possibly distinct from *H. sessilis*). *Heterotaxis fritzii* superficially resembles *H. sessilis*, but is a smaller plant overall with fleshier leaves that are laterally fused and triangular in cross section. The lip is similar in shape to that of *Heterotaxis sessilis* but with two calli (versus one callus in *H. sessilis*). Phenetically, *Heterotaxis fritzii* is, however, more similar to *H. santanae* (Carnevali & I. Ramírez) Ojeda & Carnevali, with which it shares the small vegetative size, narrow leaves, overall habit, and similar flowers. The labellum in *H. santanae* has a rounded or obtuse apex and it lacks the dark purple trans-

versal blotches found in the labellar disk of *H. fritzii*, among other floral differences. *Heterotaxis santanae*, furthermore, grows on the eastern side of the Andes, while the novelty here proposed is apparently restricted to the Pacific coast of northern Ecuador.

**Distribution and habitat notes.** *Heterotaxis fritzii* is poorly known, since it has only been collected a few times and only seen alive once by the authors. At the paratype locality it grew as a subterrestrial on a moist and shady road bank, along with many other orchid species (*Scaphyglottis* sp. aff. *sumersii* C. Schweinfurth, *S. prolifera* Cogniaux, *Maxillaria cymbidioides* Dodson, J. T. Atwood & Carnevali, *Epidendrum ramosum* Jacquin). The single plant found then grew slowly in cultivation in St. Louis, Missouri, for several years, but never thrived and eventually died without ever flowering again (see paratype).

**Conservation status.** Apparently a rare, narrow endemic in coastal Ecuador. Since it has no horticultural appeal, it is probably not under any particular collecting pressure.

**Paratype.** ECUADOR. **Imbabura:** 5–14 km SE of Lita along road to Ibarra, 600–850 m, plants collected along road embankments, 27 Mar. 1994, G. Carnevali & C. H. Dodson 3443 (CICY).

***Heterotaxis schultesii*** Ojeda & G. A. Romero, sp. nov. TYPE: Brazil. Amazonas: Río Urubú, between Cachoeira Iracema & Manaus–Caracarai road, 6 June 1951, G. T. Prance, D. Philcox, W. A. Rodrigues, J. F. Ramos & L. G. Farias 5023 (holotype, NY; isotypes, A, F, HB, INPA, K, MG, NY, R, S, U, US). Figures 3, 4.

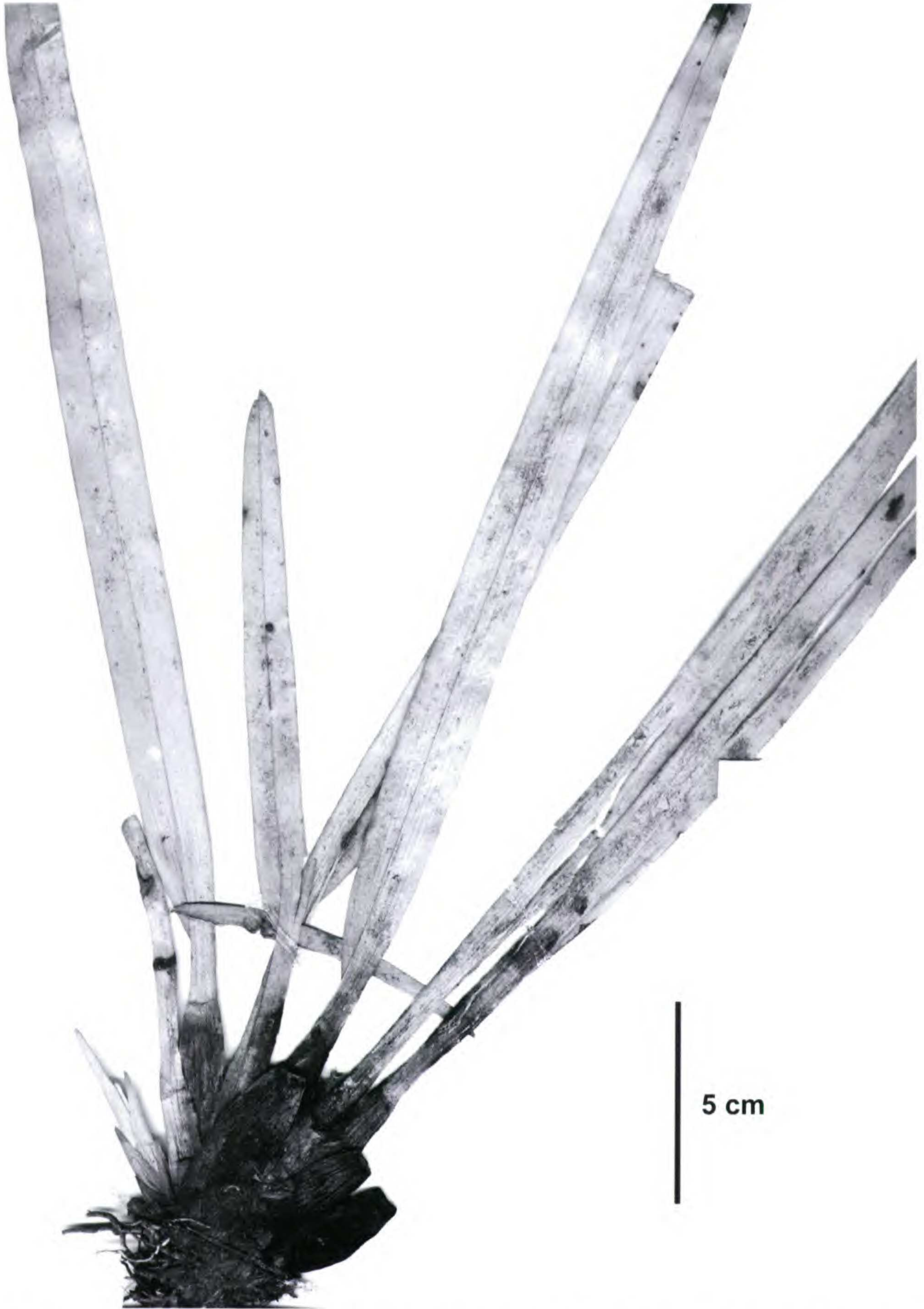


Figure 4. *Heterotaxis schultesii* Ojeda & G. A. Romero, flowering habit (based on *R. E. Schultes & I. Cabrera 17488* (AMES)).

Species haec *H. villosae* (Barbosa Rodrigues) F. Barros similis sed habitu parviore, foliis angustioribus crassioribus, apice lobis magni-inaequilateris, floribus fuscis-cinnabarinis, labello angustiore, callo biseriato carnosio abhorret.

Plant a caespitose epiphyte, erect, 20–40 cm high, rhizome abbreviated; roots grayish, about 0.2 cm diam.; pseudobulbs aggregate, 3.5–6 × 1–1.5 cm, oblong-ellipsoid and strongly compressed laterally, unevenly marked with dense longitudinal scars upon drying, unifoliate, clothed with 4 to 6 sheaths, the innermost 2 to 4 bearing foliar blades, these distichously arranged. Leaves coriaceous, erect on the pseudobulb apex, 17–28 × 1–1.7 cm, oblong, basally attenuate and forming a 1.5–6 cm long pseudopetiole, apex acute, unequally 2-lobed, the longer apical lobe 0.5–1 cm longer than the shorter, both lobes acute, inwardly oblique; leaf blades of the sheaths enveloping the pseudobulb, 1.5–5.5 × 0.8–1.5 cm, partially fused at the base (with a “y” cross section near the articulation), forming a relatively long pseudopetiole. Inflorescence 1-flowered, borne on the leaf-sheath axils; peduncle fleshy, 33–35 mm long, concealed by 5 distichous bracts, the last one surpassing the articulation of the peduncle to the ovary and pedicel; floral bract similar to peduncle bracts, membranous, ca. 5 mm long, triangular, acute, shorter than ovary; ovary and pedicel 10–11 mm long, ca. 2 mm thick. Flowers medium-sized for the genus, ca. 1.7 cm long., apparently erect on the pedicel, perianth segments subparallel to the column, yellow brown to orange or orange-red, fleshy; dorsal sepal 16–18 × 2.8–3.1 mm, lanceolate to oblong lanceolate, obtuse, lateral sepals similar to dorsal but slightly oblique; petals 14–16 × 1.8–2.1 mm, oblanceolate to spatulate, acute, the margins papillose from apex to mid-length; labellum articulate to column foot, 13.5–14.5 × 3.9–4.1 mm, slightly 3-lobed, apex obtuse to obtusely acute; disc with two calli, these fleshy, linear, the basal one originating at the base of the disc and extending to about mid-length, the apical callus borne near the attenuate point of the labellum blade and from there extending to near the apex; anther ca. 3.5 mm long, unilocular, the apical surface papillose; pollinia four, unequal; column 7–9 mm long, hemi-cylindric, arcuate, with a poorly defined foot 1–2 mm long. Fruits not seen.

*Eponymy.* Named in honor of Richard Evans Schultes, among the first collectors of this species.

*Heterotaxis schultesii* resembles *H. villosa*, but it is recognized at once by its smaller overall vegetative size (20–40 cm tall). The leaves are thicker in texture, with fewer cell layers (Ojeda, 2003) and narrower, compared to the wide leaves of *H. villosa*.

Most distinctly, the apex of the leaves is conspicuously bilobed. The apical lobes of the leaf are so strongly unequal that the larger lobe is 0.5–1 cm longer than the shorter, a dimension that equals or exceeds the width of the leaf at its apical portion. This condition is not found in any other species of *Heterotaxis*. The labellum of *H. schultesii* is similar in shape to that of *Heterotaxis sessilis*, but the two fleshy calli are different. The brownish yellow to red-orange color of the flowers is unique in *Heterotaxis*.

*Heterotaxis schultesii* is probably only distantly related to *H. sessilis*. According to our results, *H. schultesii* lies, within the genus, in a basal position (Ojeda, 2003; Ojeda et al., 2003).

*Distribution and habitat notes.* Known from a few collections made in Amazonian Brazil (Amazonas) and Colombia (Vaupés). It grows as an epiphyte, and it has been reported as occurring on savannah trees (e.g., *Garay 108*), on flooded forests (e.g., *Garay 91*) or along rivers (e.g., *Prance et al 5023*). The known collections were made at altitudes ranging from 180 to 250 m.

*Phenology.* Flowering collections have been made in the months of June, August, and September; no fruiting specimens have been examined.

*Paratypes.* COLOMBIA. **Vaupés:** Río Piraparaná (trib., Río Apaporís), Caño Teemeña, 10 Sep. 1952, *R. E. Schultes & I. Cabrera 17488* (AMES, CICY); Cerro de Yapobodá, Río Kuduyarí, 15 Aug. 1960, *L. A. Garay 108* (AMES, CICY); along Río Kuduyarí cerca de Mitú, 12 Aug. 1960, *L. A. Garay 91* (AMES); Río Kuduyarí, Yapobodá, savana con arenisca, 25 June 1958, *H. G. Barriaga, R. E. Schultes & H. Blohm 15892* (AMES); Río Apaporis entre Río Pacoa y el Río Kananarí, 21 June 1951, *R. E. Schultes & I. Cabrera 12788* (AMES); Río Apaporis entre Río Pacoa y Río Kananarí, 21 June 1951, *R. E. Schultes & I. Cabrera 12723* (AMES, K); Río Apaporis, 15 June 1952, *R. E. Schultes & I. Cabrera 16717* (AMES).

#### NEW COMBINATIONS

Phylogenetic work using ITS 1 and 2 and a suite of morphological and anatomical characters identified 11 taxa belonging in the *Heterotaxis* clade, itself part of the larger *Heterotaxis–Ornithidium* complex (Ojeda, 2003; Ojeda et al., 2003; N. H. Williams et al., in prep.). All share the generalized habit and vegetative architectures of *Heterotaxis* described above and the fleshy flowers characteristic of the *Heterotaxis–Ornithidium* complex. These species were: *Maxillaria discolor* Loddiges ex Loudon, *M. villosa*, *H. schultesii*, *M. maleolens* Schlechter, *M. violaceopunctata* Reichenbach f., *M. crasifolia*, *M. superflua*, *M. santanae* Carnevali & I. Ramírez, *H. fritzii*, *M. equitans*, and *M. valenzue-*



*lana*. As indicated above, Barros (2002) already transferred several of these taxa, all of them occurring in Brazil, to *Heterotaxis*.

Two additional species, also represented in Brazil, *Maxillaria equitans* and *M. valenzuelana*, were treated by Barros as members of the genus *Marsupiarina*. Our analysis strongly suggests that *Marsupiarina* is embedded within *Heterotaxis*, leaving a balance of six other species that are yet to be transferred to *Heterotaxis*. Of these, five species were included in the phylogenetic analysis performed by Ojeda et al. (2003), while a sixth one, the recently described *Maxillaria microiridifolia* D. E. Bennett & E. A. Christenson, although unavailable to us in the course of the present study, is clearly referable to *Heterotaxis* and closely related to (if not conspecific with) *Maxillaria santanae* Carnevali & I. Ramírez (transferred to *Heterotaxis* below). Thus, the following six new combinations are warranted:

***Heterotaxis discolor*** (Loddiges ex Lindley) Ojeda & Carnevali, comb. nov. Basionym: *Dicrypta discolor* Loddiges ex Lindley, Edwards's Bot. Reg. 25: 91. 1839. 1858. *Maxillaria discolor* (Loddiges ex Lindley) Reichenbach f., in Walp. Ann. Bot. Syst. 6: 529. 1863. TYPE: Guyana ("Demerara"). Without precise locality, ex Hort. Loddiges (holotype, K-Lindl.).

As mentioned above, *Dicrypta* is without ambiguity a nomenclatural synonym of *Heterotaxis*.

*Dicrypta bicolor* Paxton ex J. E. Planchon often had been referred to the synonymy of *Maxillaria discolor* (e.g., Foldats, 1970: 449; Carnevali & Ramírez, 2003). We recently had the opportunity to research this name, and it is evident that its nomenclatural and systematic status is unclear. First of all, the authorship of the name cited by Planchon (1858) should be "Hort. ex J. E. Planchon," and the name appears on page 159 (not "Paxt. ex J. E. Planchon" or page 73, as cited by Foldats, 1970: 449 and Carnevali & Ramírez, 2003). "*Dicrypta bicolor* Bate." was also cited in the second supplement of Loudon's *Hortus Britannicus* (Loudon, 1839: 630). However, neither Planchon (1858: 159) nor Loudon (1839: 630) validate the corresponding horticultural name (K. Gandhi, pers. comm., 2005). Furthermore, the *World Checklist of Monocots* (2004) cites "*Dicrypta bicolor* (Ruiz & Pav.) Bateman ex Loudon, Hort. Brit., ed. 3, Suppl.: 630 (1839)" as a synonym of *Maxillaria bicolor* Ruiz & Pavón, which we strongly oppose, as there is no evidence linking Bateman's plant from "Demerara" (fide Loudon, 1839: 630) to the Andean plant described by Ruiz and Pavón. At this point we de-

ferred any nomenclatural action until the status of *Dicrypta bicolor* is clarified.

***Heterotaxis equitans*** (Schlechter) Ojeda & Carnevali, comb. nov. Basionym: *Camaridium equitans* Schlechter, Repert. Spec. Nov. Regni Veg. Beih. 7: 176. 1920. *Marsupiarina equitans* (Schlechter) Hoehne, Arq. Bot. Estado de São Paulo 2: 71. 1947. *Maxillaria equitans* (Schlechter) Garay, Bot. Mus. Leaf. 18: 208. 1958. TYPE: Repert. Spec. Nov. Regni Veg. Beih. 57: t. 63, fig. 242, 1929 (lectotype, designated here). EPITYPE: Colombia. Valle: Cauca Valley, Zarzal, 970–1050 m, 21 July 1922, F. W. Pennel, E. P. Killip & T. E. Hazen 8403 (epitype designated here, AMES, NY). [The holotype, *M. Madero s.n.*, for *Camaridium equitans* was destroyed at B.]

*Camaridium vandiforme* Schlechter, Beih. Bot. Centralbl. 42: 174. 1925. *Maxillaria vandiformis* (Schlechter) C. Schweinfurth, Bot. Mus. Leaf. 11: 291. 1945. TYPE: Peru. Loreto: vicinity of Iquitos, 100 m, dense forest, on living tree, Jan.–Feb. 1937, G. Klug 10076 (lectotype, designated here, AMES). [Syntypes by G. Hübner (120, 124, 149) were destroyed at B.]

*Maxillaria matogrossensis* Brade, Arq. Serv. Florest. 1: 46, t. 3, Fig. 1–8. 1939. *Marsupiarina matogrossensis* (Brade) Hoehne, Arq. Bot. Estado de São Paulo N.S., Formato Maior 2: 71. 1947. TYPE: Brazil. "Mato Grosso": ex Hort. Jardim Botânico Rio de Janeiro, 11 June 1939, *Inspectoria Agrícola Federal da VIII Região Mato Grosso V.14.399* (holotype, RB not seen).

***Heterotaxis maleolens*** (Schlechter) Ojeda & Carnevali, comb. nov. Basionym: *Maxillaria maleolens* Schlechter, Repert. Spec. Nov. Regni Veg. Beih. 19: 233. 1933. TYPE: Costa Rica. Alajuela: Río Jesús de San Ramón, 800 m, 10°02'N, 84°31'W, June 1922, A. M. Brenes 281 (lectotype designated by Barringer, Fieldiana, Bot. n.s., 17: 10. 1986, CR-25985). [The holotype of *Maxillaria maleolens* at B was destroyed, and Barringer designated the only known isotype as the lectotype.]

***Heterotaxis microiridifolia*** (D. E. Bennett & Christenson) Ojeda & Carnevali, comb. nov. Basionym: *Maxillaria micro-iridifolia* D. E. Bennett & Christenson. Icones Orchidacearum Peruvianum. Plate 699. 2001. TYPE: Peru. Puno: Sandia, Candamo river valley, 550 m, 15 Sep. 1998, M. Cavero B. ex D. B. Bennett 7823 (holotype, Herb. Bennettianum, Lima, Peru; isotype, NY).

***Heterotaxis santanae*** (Carnevali & I. Ramírez) Ojeda & Carnevali, comb. nov. Basionym: *Maxillaria santanae* Carnevali & I. Ramírez, Ann. Missouri Bot. Gard. 76: 377. 1989. TYPE: Venezuela. Amazonas: Atabapo, Cerro Marahuaca, 11 Nov. 1986, *G. Santana 1* (holotype, VEN; isotype, MO).

***Heterotaxis valenzuelana*** (A. Richard) Ojeda & Carnevali, comb. nov. Basionym: *Pleurothallis valenzuelana* A. Richard, Sagra, Hist. Fis. Cuba 11: 234. 1850. *Maxillaria valenzuelana* (A. Richard) Nash, Bull. Torrey Bot. Club 34(3): 121–122. 1907. *Marsupiarina valenzuelana* (A. Richard) Garay, Arq. Jard. Bot. Rio de Janeiro 12: 183. 1952. TYPE: Cuba. Valenzuela, *C. Wright 3314* (holotype, P not seen).

*Maxillaria iridifolia* Bateman ex Reichenbach f., Bonplandia 2: 16. 1854. *Marsupiarina iridifolia* (Bateman ex Reichenbach f.) Hoehne, Arq. Bot. Est. São Paulo 2: 71. 1947. TYPE: Cuba, without precise locality, “Wächst bei Cohubas,” *E. F. Poeppig s.n.* (holotype, H.G. Reichenbach f. Hb., W not seen).

*Dicrypta irisphyta* Barbosa Rodrigues, Gen. et Sp. Orch. Nov. 1: 126. 1877. TYPE: watercolor in *Iconographie des Orchidées du Brésil*, Vol. 6: t. 292 (fide Barbosa Rodrigues 1996: 420; “Tab. 487” fide Barbosa Rodrigues 1877: 126) RB [Library] (lectotype, designated here; reproduced in Barbosa Rodrigues, 1996, 1: 420). [The holotype (*J. Barbosa-Rodrigues s.n.*) of *Dicrypta irisphyta* was probably destroyed at Barbosa Rodrigues’ home in Rio de Janeiro, according to P. Cribb & A. Toscano de Brito in Barbosa Rodrigues, 1996: 30–31.]

*Maxillaria valenzuelana* subsp. *angustata* J. T. Atwood, Icon. Pl. Trop. 1371. 1989. Syn. nov. *Maxillaria valenzuelana* var. *angustata* (J. T. Atwood) Senghas, Schlechter, Orchideen ed. 3, 1/B (29): 1779. 1994. TYPE: Nicaragua. Zalaya, Siuna, *F. Ortiz 612* (holotype, SEL).

As stated by Atwood in the protologue, *Maxillaria valenzuelana* subsp. *angustata* differs from the type only in the “. . . generally smaller [size of]. . . all its parts, and the scapes and flowers [that] are more exposed.” We have seen a great deal of material of this species. The variation we detected along its geographical range and within populations is considerable: we hypothesize that *M. valenzuelana* subsp. *angustata* is well encompassed within this range of size and morphological variation.

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#### Literature Cited

- Atwood, J. T. & D. Mora de Retana. 1999. Tribe Maxillarieae: Subtribes Maxillariinae and Oncidiinae (Orchidaceae). In: W. Burger (editor), *Flora Costaricensis*. Fieldiana, Bot. n.s. 40: 1–182.
- Barbosa Rodrigues, J. 1996. *Iconographie des Orchidées du Brésil*. Edited by S. Sprunger et al. Friedrich Reinhardt Verlag, Basle.
- Barros, F. 2002. Notas taxonômicas para espécies brasileiras dos gêneros *Epidendrum* e *Heterotaxis* (Orchidaceae). *Hoehnea* 29: 109–113.
- Brieger, F. G. & R. D. Illg. 1972. O grupo *Heterotaxis* do gênero *Maxillaria* Ruiz & Pavón (Orchidaceae). Pp. 93–99 in *Anais da Sociedade Botânica do Brasil—XXIII Congresso Nacional de Botânica*, Recife.
- Carnevali, G. 1991. Cytology and the pollinaria in the Maxillariinae (Orchidaceae). Master of Science Thesis in Biology, University of Missouri–St. Louis.
- & I. Ramírez. 1989. New or noteworthy orchids for the Venezuelan flora. VII. Additions in *Maxillaria* from the Venezuelan Guayana. Ann. Missouri Bot. Gard. 76: 374–380.
- & ———. 2003. Orchidaceae, *Maxillaria*. Pp. 426–454 in J. A. Steyermark, P. E. Berry, K. Yatskievych & B. K. Holst (editors), *Flora of the Venezuelan*

- Guayana, Vol. 7. Missouri Botanical Garden Press, St. Louis, Missouri.
- Christenson, E. A. 1999. *Maxillaria*, an overview. Proceedings of the 16th World Orchid Conference: 279–292.
- Dodson, C. H. 2002. *Maxillaria*. Native Ecuadorian Orchids 3: 544–574. Dodson Trust, Sarasota, Florida.
- Dressler, R. L. 1981. The orchids: Natural History and Classification. Harvard Univ. Press, Cambridge, Massachusetts.
- . 1993. Phylogeny and classification of the orchid family. Dioscorides Press, Portland, Oregon.
- Foldats, E. 1970. *Maxillaria* (Orchidaceae). Pp. 384–557 in T. Lasser (editor), Flora de Venezuela, Vol. 15, part 4. Instituto Botánico, Caracas.
- Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland & D. L. Hawksworth (editors). 2000. International Code of Botanical Nomenclature (Saint Louis Code). Regnum Veg. 138.
- Hoehne, F. C. 1947. Reajustamento de algunas especies de *Maxillarias* do Brasil, com criação de dois novos gêneros para elas. Arqiv. Bot. Estado São Paulo f.m. 2: 65–74.
- Holtzmeier, M. A., W. L. Stern & W. S. Judd. 1998. Comparative anatomy and systematic of Senghas's cushion species of *Maxillaria* (Orchidaceae). Bot. J. Linn. Soc. 127: 43–82.
- Illg, R. D. 1977. *Maxillaria brasiliensis* Brieg. & Illg, uma espécie nova de orquídeas da seção *Heterotaxis*. Pp. 239–245 in Trabalhos do XXI Congresso Nacional de Botânica. Rio de Janeiro, Brasil.
- Lindley, J. 1830–1840. Genera and Species of Orchidaceous Plants. Ridgways, London.
- Loudon, J. C. 1839. Hortus Britannicus. Longman, Rees, Orme, Brown, and Green & Longman, London.
- McLeish, I., N. R. Pearce, B. R. Adams & J. S. Briggs. 1995. Native orchids of Belize. AA, Balkema, Rotterdam.
- Ojeda, I. 2003. Filogenia del complejo *Heterotaxis* Lindl. (Orchidaceae): Evolución de la arquitectura vegetativa y de los síndromes de polinización. Tesis de Maestría, Posgrado en Ciencias y Biotecnología de Plantas del CICY. Centro de Investigación Científica de Yucatán, Mérida, Yucatán, México.
- , G. Carnevali, W. M. Whitten & N. H. Williams. 2003. Phylogeny of *Heterotaxis* Lindley complex (Maxillariinae): Evolution of vegetative architecture and pollination syndromes. Lankesteriana No. 7: 45–47.
- Planchon, J.-E. 1858. Hortus Donatensis. W. Remquet et Cie., Paris.
- Senghas, K. 1993. Maxillarinae. Pp. 1727–1776 in Brieger et al. (editors), Die Orchideen Ed. 3, Band I/B Lieferung 28, Bogen 108–111. Paul Parey, Berlin and Hamburg, Germany.
- Whitten, W. M., N. H. Williams & M. W. Chase. 2000. Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: Combined molecular evidence. Amer. J. Bot. 87: 1842–1856.
- World Checklist of Monocots (2004). The Board of Trustees of the Royal Botanic Gardens, Kew. Published on the Internet; <http://www.kew.org/monocotChecklist/> [accessed 08 May 2005].